

5. *The cranial morphology and taxonomy of the Tapinocephalid genus Struthiocephalus.*
By L. D. BOONSTRA, D.Sc.

(With Plate XVII and 6 text-figures)

The one important genus of the Tapinocephalid Deinocephalians¹ of which the cranial structure has hitherto not been adequately described is *Struthiocephalus*.

Up to date five species of *Struthiocephalus* have been created. Few details of the cranial structure were published before I re-examined the type skull² and described the two new species, *duplessisi*³ (since transferred to the new genus *Struthiocephaloides*⁸) and *akraalensis*.⁴ Of Broom's *rheederi*⁵ and Olson and Broom's *milleri*⁶ little more is known than can be gathered from Broom's sketches of the outlines of the skull and the main skull openings—temporal fossae, orbits, nostrils and the pineal foramen.

In the collection of the South African Museum there is, besides the type skulls of *whaitsi* (S.A.M. 2678), and *akraalensis* (S.A.M. 3719), an excellently preserved skull of the species *whaitsi* (S.A.M. 11591) showing nearly all the features of the dorsal, lateral, occipital and palatal surfaces and the right side of the brain-case, and a juvenile skull (S.A.M. 11493) of the same species. The skull of the mounted specimen which has associated with it much of the postcranial skeleton (S.A.M. 3012) is crushed and shows little of the detailed structure.⁷

The structural details determined in these five specimens are here pooled to give an account of the cranial morphology of the genus but the figures are all of the one specimen of *whaitsi* (S.A.M. 11591).

THE GENERAL SHAPE AND FORM

The generic name very aptly describes the shape of the skull as being very similar to the shape of the head of an ostrich. Anterior to the orbital border the snout is anteriorly directed, long, shallow but fairly broad and, in relation to the part of the skull posterior to the orbits, appears weak. With the lower jaw occluded the muzzle appears much less weak as the mentum is quite massive. The skull is low—the width over the quadratojugals being much greater than the height in this plane. The bones of the posterior part of the skull are all strongly pachyostosed, whereas those of the snout are only relatively moderately thickened with the outer bone surface smooth. The transition from the posterior part of the dorsal surface to the dorsal and lateral surface of the snout is thus abrupt but less abrupt than in *Mormosaurus*. As the strong pachyostosis does not include the lacrimal and only affects the posterior part of the prefrontal the transition from the smooth snout to the rough posterior part lies further back than in *Taurocephalus* and *Mormosaurus*. The pachyostosis in *Struthiocephalus* is not general over the posterior part of the outer surface—the 'cheek' being still

fairly light and its surface smooth, and on the dorsal surface the strong thickening is still localized, emanating from distinct centres. The pachyostosis forms a strong rugose, dorsally somewhat bulbous, postorbital bar; a prominent rugose boss surrounding the pineal foramen and a peculiar naso-frontal boss. (The first is reminiscent of the condition in the Titanosuchid *Anteosaurus*, where it is very strongly developed, and the last a feature which it has in common with the Tapinocephalid *Keratocephalus*.)

The orbits, situated in the posterior half of the skull, are large, round and directed forwards and outwards with the thickened postero-dorsal half of the orbital border strongly overhanging.

The nostrils are large and elongated, situated on the dorsal surface mainly dorsally, and only slightly laterally directed and are well back from the anterior edge of the snout, close to each other and separated by a strong internasal bar.

The temporal fossa is fairly large, higher than long, and the pachyostosis of the postorbital bar and the posttemporal arch has not reduced its size much; its antero-posterior diameter is still greater than in *Mormosaurus* and much greater than in the slitlike fossa of *Tapinocephalus*. Dorsally, it extends medially to form a bay encroaching into the parietal region (in *akraalensis* the fossa approaches the condition in *Mormosaurus*).

The interparietal width is moderate, due to a pinching-in laterally of the parietals to form the dorso-median bay of the temporal fossa.

Due to the forward position of the quadrate, which lies anterior to the plane of the orbit, the lower jaw is short and the maximum gape of the jaws is comparatively small.

The anterior teeth of the upper jaw are directed much anteriorly but the intermeshing teeth of the dentary are directed dorsally.

THE BONES OF THE DORSAL AND LATERAL SURFACES (figs. 1 and 2)

The matrix of the *Tapinocephalus*-zone being notoriously intractable, the determination of sutures in most specimens from this horizon is extremely difficult. Thus Haughton in his description of *S. whaitsi* and Broom in the case of *S. rheederi* and Olson and Broom in *S. milleri* have, together, only figured parts of two sutures. It has only been through a laborious process of 'artificial weathering' by dilute hydrochloric acid that I have been able to determine most of the sutures, but some still remain indeterminable and others uncertain.

The premaxillaries (P.Mx.) together form a large part of the snout. From the anterior border they stretch posteriorly to past the middle of the skull. From its anterior border each premaxilla narrows, where it forms the inner border of the nostril, then it stretches as a long tapering bone posteriorly, where it lies in a groove of the nasals.

The nasals (N.) are long, narrow bones, which in their postero-median part are grooved to house the posterior tongue of the premaxillaries; posterior to the limits of the premaxillaries they meet on the dorsal surface in the median

line and are here thickened to form the anterior and major part of the naso-frontal boss.

The septomaxillaries (S.Mx.) appear to be small splint-like bones forming the outer border of the nostrils, but their limits are uncertain in most specimens.

The maxillaries (Mx.) are the largest bones of the snout, being long but shallow. Posteriorly a dorsal prong just meets the prefrontal, but in some specimens the lacrimal is intercalated, and a ventral prong extends far posteriorly with its upper edge applied to the lower border of the jugal. In between these two prongs lie the anterior ends of the lacrimal and jugal.

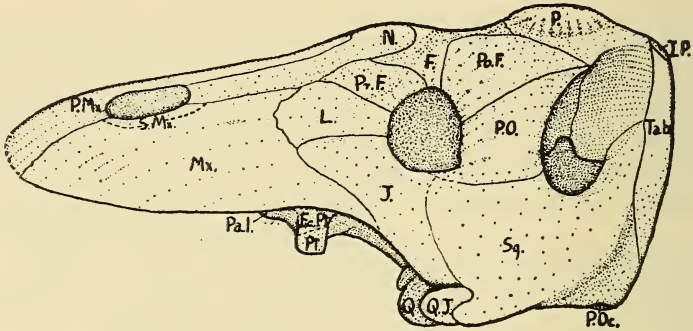


FIG. 1. *Struthiocephalus whaitsi*. Lateral view of the skull (S.A.M. 11591) ($\times \frac{1}{2}$). All the figures are not perspective drawings but projections drawn with the aid of a pantograph. The lateral view of the skull and that of the braincase are projected on to the median (sagittal) plane, the dorsal and ventral views are projected on to the plane of the alveolar border, and the occipital view at right angles to the plane of the alveolar border.

The lacrimal (L.) ventrally meets the upper edge of the jugal in a straight suture and these two bones together extend anteriorly into the posterior fork of the maxilla. The lacrimal is in its anterior extent as in *Mormosaurus* and thus stretches much further anteriorly than it does in *Taurocephalus*. It forms only a small part of the relatively unthickened anterior orbital border. Dorsally the prefrontal does not, in S.A.M. 11591, altogether exclude the lacrimal from contact with the nasal; in the other specimens a tongue of the prefrontal is intercalated between the nasal and lacrimal. (In *Taurocephalus* the lacrimal does not meet the nasal, but in *Mormosaurus* it does.)

The jugal (J.) is a strong bone; like the bones of the snout it is not greatly thickened and its surface is not rugose but smooth. It forms the antero-ventral comparatively unthickened border of the orbit. It extends far ventrally as a tapering element to be separated (in S.A.M. 11591) from the quadratojugal by a narrow incisure. Anteriorly it stretches far as a prolongation, with the lacrimal, into the posterior fork of the maxilla. The posterior border forms a shallow curve and is thus not deeply indented by an anterior wedge of the squamosal as in *Mormosaurus* and *Taurocephalus*.

The prefrontal (Pr.F.) is much thickened along its lateral edge to form the antero-dorsal thick, rugose and rounded portion of the orbital border. In all the specimens, except S.A.M. 11591, it has an anterior tongue which separates the lacrimal from the nasal. It does not extend much posteriorly, but is thickest here. Medially it is thinner and there is thus a hollow between the thickened orbital border and the naso-frontal boss.

The frontal (F.) is a large element of the dorsal skull roof. Its median part is roughly rectangular and from here three tongues extend: one, anteriorly inter-

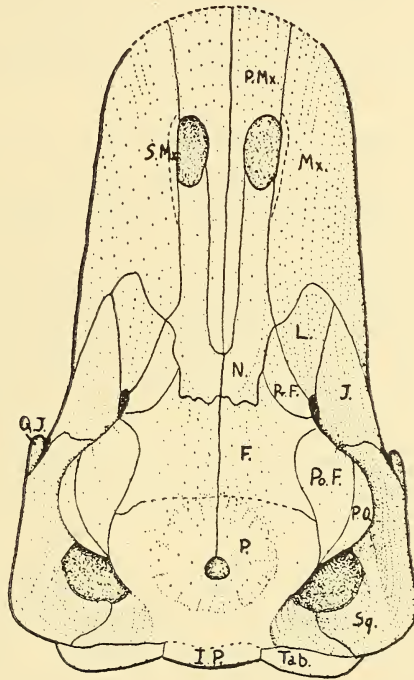


FIG. 2.—*Struthiocephalus whaitsi*. Dorsal view of the skull (S.A.M. 11591) ($\times \frac{1}{4}$).

calated between the nasal and prefrontal; the second, entering the thickened rugose upper orbital border and, the third, is a wedge between the postfrontal and the parietal. Anteriorly, the frontals meet the nasals and here form the posterior minor part of the naso-frontal boss. For the rest the frontals are not greatly pachyostosed and in *whaitsi* form a shallow saddle between the naso-frontal and parietal bosses, whereas in *akraalensis* the frontals are thickened in the median line with laterally a deep depression which is further laterally bounded by a strong ridge formed by the postfrontal and postorbital. Posteriorly, the frontals meet the parietals in a nearly straight frontal suture just anterior to the parietal boss surrounding the pineal foramen.

The postfrontal (Po.F.) forms the dorso-posterior corner of the orbital border which is here greatly thickened and very rugose. Its suture with the postorbital is in most specimens uncertain but in *whaitsi* (S.A.M. 11591) it is a large bone forming the dorsal swollen part of the postorbital bar, and in *akraalensis* it forms part of the ridge lying lateral to the depression in the surface of the frontal. This identification of the large size of the postfrontal in *Struthiocephalus* leads one to suspect that this element is a much larger bone than it has hitherto been thought to be in most Tapinocephalia. The pachyostosis of the postfrontal has resulted in the postorbital being practically excluded from the dorsal surface of the skull and thus forms only the lower part of the postorbital bar. Another result of the thickening of the postfrontal has been that together with the enlarged and thickened prefrontal the frontal tends to become excluded from the orbital border.

The parietals (P.) together form the greater part of the cranial roof. In their antero-median portion a large elevated and rugose boss is developed and is pierced by a large round pineal foramen. In their posterior half the parietals form a narrowed dorsal surface as they are here laterally pinched in. This pinching-in is less evident in *akraalensis*. Here a sharp edge separates the dorsal surface from a lateral surface, which forms the dorsal part of the median or inner face of the temporal fossa. This lateral parietal surface, extending on to the posttemporal arch to meet the squamosal, effectively prevents the postorbital from meeting the squamosal at this level. The medio-dorsal bay of the temporal fossa thus formed by the pinching-in of the parietals laterally is clearly shown in *whaitsi*, but in *akraalensis* the temporal fossa is more a continuous slit with this bay not clearly demarcated. Posteriorly, the parietals are buttressed by the interparietal in their median part and, more laterally, by the strong tabulars.

The postorbital (P.O.) is a massive element forming the lower part of the thickened postorbital bar which in its upper postfrontal part is bulbous on a scale just less than in the Titanosuchid *Anteosaurus*. The postorbital bar is strong, wide and fairly rugose in *whaitsi*, and very strong, very wide and strongly rugose in *akraalensis*. Posteriorly, the postero-lateral flange of the parietal lies between the posterior process of the postorbital and the squamosal. In a juvenile specimen of *whaitsi*, S.A.M. 11493, the posterior process of the postorbital still stretches far posteriorly, but even here does not meet the squamosal. Ventrally, the postorbital forms an overlapping suture with the squamosal.

The squamosal (Sq.) is the main constituent bone of the 'cheek'. It is a strong thickened element but, as in the jugal, its outer surface is not rugose but smooth in *whaitsi*, but with pits and rugae in *akraalensis*. Anteriorly, it meets the jugal in a long curved suture with no anterior wedge-shaped process as in *Mormosaurus* and *Taurocephalus*. Its postero-ventral corner overlaps on the outer surface of the quadratojugal. Dorsally, it is overlapped by the ventral edge of the postorbital, and, further, posteriorly, it forms the thickened lower border of the temporal fossa. From here it sweeps upwards to form most of the anterior

face of the posttemporal arch and here its dorsal end overlaps the postero-lateral flange of the parietal, where this bone forms the inner upper margin of the temporal fossa. Postero-ventrally, the squamosal forms the thickened rounded postero-ventral edge of the skull. This rounded border forms the lateral wall of the wide and deep auditory groove, which groove lies mostly in the squamosal. Medially to this groove, the squamosal forms a strong and prominent ridge, medio-ventrally buttressed by the paroccipital and further dorsally wholly formed by the tabular. This ridge, thus composed of squamosal, tabular and paroccipital, forms the median wall of the auditory groove and from it originated the strong depressor muscle of the mandible.

The tabular (Tab.) in dorsal view is seen to form the posterior half of the dorsal part of the posttemporal arch, supporting the anterior half formed by the flange of the parietal and the up-sweeping flange of the squamosal. In lateral view, the tabular is seen to form the lateral part of the posterior edge of the skull.

The interparietal (I.P.) in dorsal view, shows its upper edge where it forms the posterior buttress to the parietal in the median part of the posterior margin of the skull.

The quadratojugal (Q.J.) in dorsal and lateral views is seen to form the antero-ventral corner of the 'cheek'. Along its posterior border it is clasped by the squamosal and its inner surface supports the quadrate. Its dorsal margin does not abut against the jugal but is separated from it by a narrow incisure.

THE OCCIPUT (fig. 3)

The occiput in *Struthiocephalus* forms a large surface, much broader than high and nearly semicircular in outline. It is shallowly concave from side to side.

In the median line it is nearly vertical with its dorsal edge slightly further posteriorly and here it lies in a plane nearly at right angles to the plane of the maxillary alveolar border. In the median line there is a ridge, which runs from the *foramen magnum* to the upper edge of the occipital surface. In *whaitsi* this ridge is wedge-shaped, broad dorsally and tapering to the upper edge of the *foramen magnum*, whereas in *akraalensis* this ridge is straight and narrow with a sharp

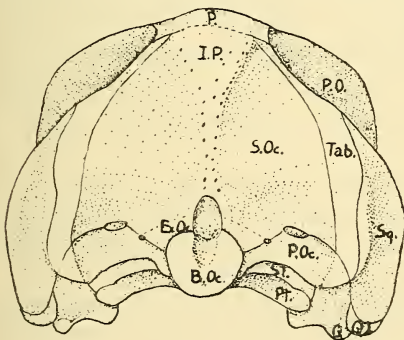


FIG. 3.—*Struthiocephalus whaitsi*. Occipital view of the skull (S.A.M. 11591) ($\times \frac{1}{4}$).

edge forming the median line with a deep depression lateral to it. In this species the occiput has its ventral part situated much anteriorly so that it is no longer nearly at right angles to the alveolar border but forms an obtuse angle with the alveolar plane and an acute angle with the dorsal surface. This may be due to post-mortem dorso-ventral pressure.

The condyle is directed postero-ventrally so that the skull would normally hang somewhat downwards. It forms a stout rounded knob, dorsally excavated by a groove leading into the *foramen magnum*. The *foramen magnum* is large and oval. The posttemporal fossae are small slits, bounded dorsally by the supraoccipital and ventrally by the paroccipital. The lateral outer border of the occipital plate is formed by the squamosal and median to this lies the deep auditory groove, whose inner wall is formed by a strong and prominent ridge to whose formation the tabular, squamosal and paroccipital contribute. Ventrally the condyles of the quadrates lie far anteriorly to the plane of the occiput. In occipital view the basioccipital condyle forms the median part of the ventral edge, and laterally the quadrate rami of the pterygoids together form a third of the ventral edge of the skull.

In only one specimen (S.A.M. 11591) is the occiput well preserved, and even here the sutures between the basioccipital and exoccipital and between the supraoccipital and interparietal cannot be determined.

The basioccipital (B.Oc.) apparently forms the whole of the condyle with no participation by the exoccipital, which appears to be a small element lying dorso-laterally in a plane anterior to that of the condyle. A groove on the dorsal surface of the basioccipital leads into the *foramen magnum*. A notochordal pit lies in the centre of a shallow concavity in the postero-ventral surface of the condyle.

The supraoccipital (S.Oc.) appears to form the major part of the median portion of the occipital plate. Laterally it stretches to the inner base of the prominent ridge composed of the tabular, squamosal and paroccipital and forming the inner rampart of the auditory groove, and here it meets the tabular in a long vertical suture. In its ventro-lateral part the supraoccipital forms the upper border of the slit-like posttemporal fossa. Medially and laterally to the posttemporal fossa it meets the paroccipital and enters the upper edge of the jugular foramen. Dorsally its junction with the interparietal cannot be determined, but with this bone it forms the median occipital ridge to which it contributes the lower, narrower part.

The interparietal (I.P.) forms the dorso-median part of the occiput but it is uncertain how far it stretches ventrally before meeting the supraoccipital. It forms the dorsal part of the median ridge, which, in *whaitsi*, is broad in its interparietal part but in *akraalensis* is sharp and narrow throughout.

The tabular (Tab.) as I have determined its limits, forms only a small part of the occipital surface as it appears not to stretch far medially. It forms the greater part of the prominent lateral ridge lying medially to the auditory groove. Dorsally the tabular flanks the postero-lateral parietal flange and the upsweeping dorsal squamosal flange and thus forms the postero-dorsal part of the temporal arch. This part of the tabular is especially strong in *akraalensis*, and here its dorsal edge is wide, strong and rugose.

The paroccipital (P.Oc.) in occipital view is seen to be a strong bar medially abutting against the basioccipital and stretching laterally to the lateral ridge

where its dorso-lateral corner forms the most prominent part of this ridge. Its ventro-lateral edge overlaps and supports the quadrate and dorsally it meets the supraoccipital and forms the lower border of the small slit-like posttemporal fossa and that of the small *foramen jugale*. Medially to the jugular foramen it meets the ventral edge of the exoccipital.

The quadrate (Q) in occipital view shows a squarish posterior surface with, ventrally, paired strong rounded knobs separated by a broad groove together forming the ginglymoid articular surface for the articular. Laterally the quadrate is overlapped by the squamosal and flanked by the quadratojugal. Dorsally the posterior face of the quadrate is overlapped by the paroccipital. Medially the long quadrate ramus of the pterygoid is applied to its inner surface ventral to where the expanded distal end of the stapes abuts against the quadrate.

The quadratojugal (Q.J.) in posterior view is seen to form the latero-ventral corner of the skull. Dorsally its posterior surface is overlapped by the squamosal.

The stapes (St.) is only partly exposed in occipital view. It is a stout rod with its proximal end obscured by the paroccipital and its distal expanded end is seen to be applied to the inner face of the quadrate.

The pterygoid (Pt.) only shows its long quadrate ramus in occipital view. This is seen to extend very far posteriorly with its dorsal edge overlapping the distal end of the stapes and its postero-lateral end applied to the inner face of the quadrate.

If my interpretation of the relations of the interparietal, supraoccipital, tabular and paroccipital is correct the structure of the occiput in *Struthiocephalus* differs greatly from the condition in *Mormosaurus*, *Taurocephalus*, *Tapinocephalus* and *Moschops*. In these forms the tabular has a much greater occipital surface and the supraoccipital is a much smaller bone. In *Taurocephalus* and *Moschops* the tabular forms the whole of the dorsal border of the posttemporal fossa, but in *Tapinocephalus* the tabular, as in *Struthiocephalus*, is excluded from the posttemporal fossa.

THE VENTRAL SURFACE OF THE SKULL (fig. 4)

The palate and the *basis cranii* lie in the same plane, with the strong lateral pterygoidal rami extending ventral to this plane and the suspensorium lying still further ventrally. Striking is the very anterior position of the articular surfaces of the quadrates, which lie anterior to the posterior third of the skull. The suborbital fossae are small, the *choanae* large and oval and the interpterygoid vacuity is a narrow slit not extending between the prevomers.

The basioccipital (B.Oc.), in ventral view, is seen to carry a strong condyle pear-shaped in outline. Postero-ventrally the condyle is circularly excavated round the notochordal pit. Anteriorly to the condyle the basioccipital forms a squarish plate of bone directed antero-ventrally to meet the surface of the basisphenoid at an obtuse angle in a not very secure ankylosis. This surface carries a low median ridge flanked by shallow oval depressions and the anterior and lateral edges are rounded. Laterally the basioccipital is flanked by the

small exoccipital, whose limits are uncertain. Anterior to the jugular foramen the basioccipital is strongly supported by the paroccipital which it meets in a firm curved suture.

The basisphenoid (B.Sph.) posteriorly meets the basioccipital at an angle so that the two ventral surfaces subtend an obtuse angle. The postero-lateral corner of the basisphenoid forms the anterior border of the *foramen ovale*. Anteriorly the basisphenoid extends as a blunt wedge in between the pterygoids but the exact position of the suture is uncertain and its probable position is

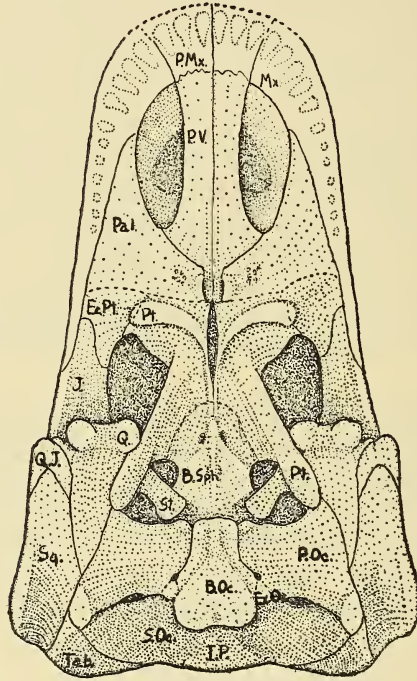


FIG. 4.—*Struthiocephalus whaitsi*. Ventral view of the skull (S.A.M. 11591) ($\times \frac{1}{6}$).

given in broken lines. In the median line the basisphenoid carries a low, sharp keel, lateral to whose anterior end lie the carotid foramina.

The pterygoids (Pt.) form a large part of the ventral surface. In the middle of the skull each pterygoid consists of a thin plate of bone meeting the basisphenoid obliquely along a long edge whose exact position has not been determined but which I believe stretches in anterior direction to the median line from the notch leading into the pituitary fossa. In the median line the pterygoid meets its fellow to form a sharp median keel. Anterior to this keel lies the interpterygoid slit. Lateral to the median keel the pterygoid is deeply excavated and lateral to this wide and deep groove lies the quadrate ramus of the pterygoid. This is a deep sheet of bone lying obliquely in the skull nearly at right

angles to the plane of the palate. The quadrate ramus extends far posteriorly and here its outer surface is applied to the inner face of the quadrate, well behind the plane of the condyle of the quadrate, and there is thus no anterior process of the quadrate to meet the pterygoid. The distal end of the stapes thus passes over the upper edge of the quadrate ramus of the pterygoid to reach the medial face of the quadrate. In no other Deinocephalian is the quadrate ramus of the pterygoid known to extend so far posterior to the quadrate condyle, which fact emphasizes how far the quadrate has shifted in an anterior direction.

The lateral ramus of the pterygoid is only moderately strong and has no great ventral extent. This is in strong contrast to the condition in the Titanosuchids where the ramus is very strongly developed. In *Struthiocephalus* the ramus does not extend far laterally as it does in *Taurocephalus* and all the Titanosuchids. The lateral edge of the ramus is supported by a descending process of the ectopterygoid, which, on account of the narrowness of the lateral pterygoid ramus, has a greater palatal face than in all other Deinocephalians. As in all Deinocephalians the lateral ramus is connected with the quadrate ramus by a web of bone reducing the size of the suborbital vacuity of which it forms the antero-medial border. Anteriorly the exact limits of the pterygoid are indetermined but are probably as indicated by broken lines in the figures.

The ectopterygoid (Ec.Pt.) has a larger palatal surface than in other Deinocephalians. Its anterior and median limits are not clearly shown but it appears to descend along the lateral edge of the lateral pterygoid ramus which it buttresses. Its posterior edge forms the antero-lateral border of the suborbital fossa. Postero-laterally it abuts against the jugal in a sigmoid suture and laterally against the maxilla.

The palatine (Pal.), from where the suture with the pterygoid and ectopterygoid appears to lie, stretches antero-laterally as a thickened bone to form the rounded lateral two-thirds of the choanal border, and has its lateral edge applied to the inner maxillary surface where it flanks the alveolar border. Near the median line the palatine ends with a short sharp ridge running parallel to the median line. The two palatines thus do not meet each other, as median to their inner ridged borders a posterior tongue of the prevomers intervenes. Just lateral to the ridged inner edge there lies a rounded mound on which there are indications of the roots of a small number of small palatine teeth.

The prevomers (P.V.) are strong elements together forming a massive interchoanal bar. Anteriorly they underlie the inner surface of the premaxillaries with their anterior edges bevelled. Posteriorly they widen and overlie the palatines postero-laterally and in the median line send a tongue posteriorly in between the ridged inner edges of the palatines. Anteriorly the median suture is open and the interchoanal bar is here grooved, whereas in the posterior half of the bar a keel is developed along the median line.

The premaxillary (P.Mx.) alveolar border is very massive. Each premaxilla carries three strong teeth which are directed antero-ventrally. Posterior to the functional teeth there are indications of crowns which may be either replacing

or replaced teeth. In a juvenile specimen of *whaitsi* (S.A.M. 11493) where the crowns of the teeth are just erupting the labial edge of the premaxillaries is sharp and appears to form a cutting edge functioning as such until the teeth are sufficiently developed.

The maxilla (Mx.) has its alveolar border anteriorly massive and wide but then it tapers rapidly in posterior direction, and behind the last tooth a sharp edge is continued by the jugal, sweeping down towards the quadrato-jugal. Stumps of teeth and infilled alveoli in most specimens show that there were ten to eleven maxillary teeth. The anterior four are large, the fifth appreciably smaller, the sixth abruptly smaller and the series then decreases gradually in size in posterior direction. In the juvenile specimen of *whaitsi* (S.A.M. 11493) the labial edge of the maxilla, as is the case in the premaxilla, is sharp and during immaturity apparently forms a cutting edge.

The jugal (J) in ventral view has a narrow and deep flange of bone sweeping from the sharp outer edge of the maxilla down towards the quadratojugal. Internally and dorsally to this sharp edge the jugal is thickened and extending internally forms the lateral border of the suborbital fossa, and anteriorly it meets the ectopterygoid in a sigmoid suture.

The quadrate (Q) has its articular condyle very prominent in ventral view as this forms the most ventral part of the skull. The articular surface has a median trochlear surface bounded internally and externally by longitudinally oval condyles. The rounded articular surfaces are sharply demarcated from both the posterior and the anterior face of the upper part of the bone. Laterally a ridge bounded medially and laterally by a groove lies lateral to the condyle in the plane of the ventral edge of the quadratojugal. Dorsally the posterior surface of the quadrate is seen wedged in between the paroccipital internally and the quadratojugal and squamosal externally. Internally the long quadrate ramus of the pterygoid is applied to the medio-posterior face of the quadrate. The extremity of the ramus extends far posteriorly of the plane of the quadrate condyle and there is no anterior process of the quadrate to meet the quadrate ramus of the pterygoid. No *foramen quadrati* could be located with certainty but it may be small and may lie just medio-dorsally of the ridge on the quadrate lying laterally to the condyle.

The stapes (St.) is in position in S.A.M. 11591 on both sides. It is a stout rod with expanded distal and proximal ends. The distal end applied to the inner face of the quadrate is underlain by the long quadrate ramus of the pterygoid and has its postero-distal corner much expanded. No foramen can be determined.

The quadratojugal (Q.J.) in ventral view is seen to form the angle of the 'cheek'. Its ventral edge lies in a plane dorsal to the condyle of the quadrate from which it is separated by a ridge bounded on both sides by a groove. The posterior surface of the quadratojugal is seen to be overlapped by the descending posterior squamosal process.

The squamosal (Sq.) in ventral view forms the outer edge of the posterior third of the skull. Median to this edge lies the auditory groove whose inner wall is formed by a ridge formed by the squamosal, paroccipital and tabular. Further ventrally the squamosal supports the posterior face of the quadratojugal and quadrate.

The paroccipital (P.Oc.) shows a much greater face in ventral view than it does in occipital view. This rotation of the paroccipital from the occipital plane on to the ventral surface is one of the results of the forward shift of the quadrates and is a character distinguishing all Deinocephalians from the other Therapsids.

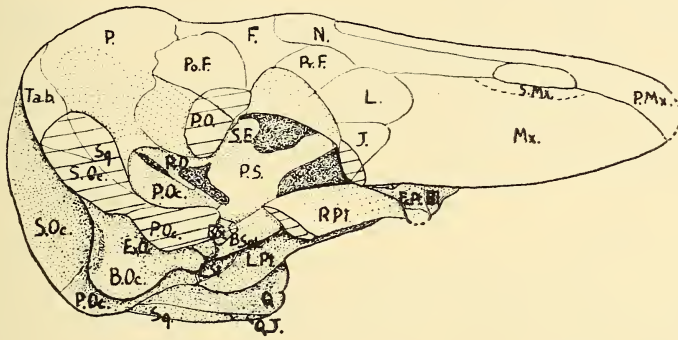


FIG. 5.—*Struthiocephalus whaitsi*. The right side of the braincase in lateral view (S.A.M. 11591) ($\times \frac{1}{8}$). The suborbital bar, postorbital bar and occipital plate fractured and here seen in section. The right quadrato ramus of the pterygoid and the right stapes are also seen in section where they have been fractured.

The paroccipital is a strong massive element acting as a very firm connecting link between the bones of the 'cheek' and the suspensorium lying laterally and the basioccipital of the cranial base. Posteriorly the thickening of the paroccipital and supraoccipital have all but obliterated the posttemporal fossa which is only preserved as a narrow slit. The postero-lateral corner of the paroccipital forms the most prominent part of the strong ridge from which the depressor mandibulae originates. Antero-medially the paroccipital forms the posterior half of the border of the *foramen ovale*.

In ventral view the tabulars, interparietal and supraoccipitals are seen to lie well posterior to the basioccipital condyle with the first two forming the posterior edge of the skull which, as is the case in most Tapinocephalids, is nearly a straight line, whereas in the Titanosuchids this edge is concave. In *akraalensis* more of the occiput is seen in ventral view than is the case in *whaitsi*.

THE BRAINCASE IN LATERAL VIEW (fig. 5)

In a specimen of *whaitsi* (S.A.M. 11591) a fracture through the posttemporal arch, postorbital and suborbital bars has enabled me to prepare the lateral surface of the braincase on the right side. But after the removal of the intractable

matrix from the temporal fossa and orbit the surface of the internal bones thus exposed is not sufficiently clear so as to determine the limits of the constituent bones with any great degree of certainty. The accompanying figure shows what structural details have been determined. The parasphenoid (P.S.) is the largest element forming a large part of the fenestrated septum. A dorsal sheet of bone supports the ventral edge of the sphenethmoid and a well-developed anterior process is directed obliquely forwards. Of this part of the parasphenoid Efremof says that in many cases, 'den vordere Forsatz des Parasphenoid knorpelig blieb', whereas in fact the parasphenoid is an *os investitiens* and thus not an element preformed in cartilage.

Of the sphenethmoid (S.E.) only the lower part can be seen where it rests on the upper edge of the dorsal parasphenoidal process.

The prootic (P.O.) is seen wedged in the postero-dorsal corner and its relations with the sphenethmoid are uncertain.

The opening for the trigeminus and the fenestra of the fossa hypophyseos are situated as shown in the figure.

THE LOWER JAW

In S.A.M. 11693 most of the dentaries are preserved and in S.A.M. 11493 the crushed posterior half of the right mandibular ramus is present, but in both only the outer surface could be prepared. What could be determined of the structure I have included in the composite figure accompanying the description of *Struthiocephaloides duplessisi*.

The hinge of the lower jaw lies very far forward, in the plane of the orbit. The dentary forms nearly two-thirds of the ramus and its mentum is massive and fairly upright. The teeth are directed upwards and only slightly outwards to intermesh with the labially directed teeth of the upper jaw. The angular has a large outer flange and the surangular has a strong rounded dorsal border curving upwards and forwards from the articular.

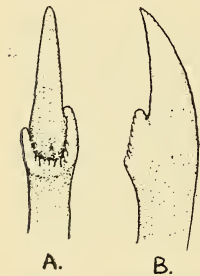


FIG. 6.—*Struthiocephalus whaitsi*. A tooth of the lower jaw (S.A.M. 11591) ($\times \frac{1}{2}$). a, lingual view. b, lateral view.

THE DENTITION (fig. 6)

In all specimens stumps, imperfect crowns and empty alveoli are all that are preserved. In fragments of the lower jaw of S.A.M. 11591 a few crowns of the teeth of the lower jaw are preserved and one is figured here.

All the teeth have a labial talon or pointed cusp at whose base there lies lingually a cup-shaped base with a serrated edge.

The three teeth in the premaxilla and the first four maxillary teeth are large with long labial cusps. Then abruptly the fifth tooth is much smaller with a short labial talon and then the rest of the teeth decrease still further in size posteriorly.

A tooth just erupting in the lower jaw (S.A.M. 11591), which is thus as yet unabraded, shows three longitudinal ridges on the lingual surface of the talon. With use the talon is abraded and the ridges disappear. Through use the serrations on the labial edge of the cup are also worn down and lost.

There are indications that in the anterior teeth there can be at least three successive sets of teeth.

TAXONOMIC DIAGNOSES

As Mormosaurids I have grouped together (1936) the genera *Mormosaurus*, *Struthiocephalus* and *Taurocephalus*. The following amended diagnosis for this group is suggested: Skull large, long and moderately wide; snout long or fairly long and shallow; cranial bones strongly thickened with parietal, naso-frontal and postorbital bosses undeveloped, distinctly developed or tending to coalesce in the general pachyostosis; postorbital bar moderately wide to wide and massive; the facial surface fairly or very abruptly demarcated from the thickened cranial surface; temporal fossae fairly small with the dorso-ventral diameter appreciably or not very much greater than the antero-posterior; intertemporal region fairly narrow to moderately wide and laterally distinctly or only slightly bayed; parietals entering supratemporal border; quadratus ramus of the pterygoid extending only up to or well posterior to the quadratic condyle, which is situated far forward; tabular entering or not entering the post-temporal fossa; no differentiation of teeth into incisors, canines and postcanines.

GENERIC DIAGNOSES

A. *Mormosaurus*

1. Snout short, very shallow, facial surface not extending posterior to the anterior orbital border, very abrupt transition from the facial to the cranial surface.
2. Dorsal cranial surface very strongly pachyostosed, with the centres of thickening coalesced and transition on to face very abrupt along a very definite transverse line forming a transverse wall.
3. Additional pachyostosis:
 - a. Nasal boss laterally confluent with the thickening of the postorbital bar and the prefrontal and thus forming a transverse wall from orbit to orbit.
 - b. Parietal boss not very distinct, confluent with the general pachyostosis of the parietal and frontal.
 - c. Postorbital bar wide and massive but without distinct bulbous boss and thus flowing evenly on to the general dorsally thickened surface.
 - d. Posttemporal arch greatly thickened and rugose.
 - e. Orbits not visible in dorsal view and in dorsal view the postorbitals do not form the lateral border of the skull.
 - f. Antero-posterior diameter of temporal fossa small and fossa transversely oval.
 - g. Dorsal parietal surface fairly wide, laterally indistinctly bayed.

4. Dentition feeble, uniform.
5. Quadrate moderately far forward with the quadrate ramus of the pterygoid not extending much posterior to the plane of the quadratic condyle, not underlying the distal end of the stapes.
6. The lateral ramus of the pterygoid does not form a prominent transverse bar and the width across the transverse rami is small.
7. The intersquamosal width is large.
8. The basioccipital condyle is directed posteriorly.
9. The frontal appears to be small and is excluded from the orbital border, the supraoccipital is wide and low, the tabular with a moderate occipital face and apparently enters the posttemporal fossa, the lacrimal meets the nasal, the squamosal with an anterior wedge into the jugal. (This diagnosis is based on Watson's description and figures.)

B. *Struthiocephalus*

1. Snout long, shallow, facial surface extending far back, posterior to the anterior orbital border, fairly abrupt transition on to the cranial surface.
2. Dorsal cranial surface strongly pachyostosed, but centres of greatest thickening still distinct and the transition on to the face fairly abrupt but not along a definite line and thus not forming a transverse wall.
3. Additional pachyostosis:
 - a. Naso-frontal boss not laterally confluent with the pachyostosis of the postorbital bar and the prefrontal and thus not forming a transverse wall from orbit to orbit.
 - b. Parietal boss distinct.
 - c. Postorbital bar moderately wide to wide, fairly massive to massive, with or without distinct bulbous boss and with or without a ridge demarcating it from the dorsal surface.
 - d. Posttemporal arch moderately to greatly thickened, fairly smooth to rugose.
 - e. Orbits just visible in dorsal view, and in dorsal view the postorbitals do not form the lateral border of the skull.
 - f. Antero-posterior diameter of temporal fossa moderate to fairly small and fossa oval to slitlike.
 - g. Dorsal parietal surface narrow to moderately wide, laterally distinctly or indistinctly bayed.
4. Dentition well developed with 14 teeth of which 3 are on the premaxilla; the fifth maxillary tooth is abruptly smaller than those anterior to it and then posteriorly the series gradually decreases in size.
5. Quadrate far forward with the quadrate ramus of the pterygoid extending much posterior to the plane of the quadratic condyles, underlying the distal end of the stapes.
6. The lateral ramus of the pterygoid forms a strong and prominent bar but the width across the transverse rami is small.

7. The intersquamosal width is moderate to fairly moderate.
8. The basioccipital condyle is directed postero-ventrally.
9. The frontal is of medium size and enters the orbital border, the supraoccipital is wide but apparently fairly high, the tabular with a small occipital face and excluded from the posttemporal fossa, the lacrimal meets or does not meet the nasal, the squamosal without anterior wedge into the jugal.

C. *Taurocephalus*

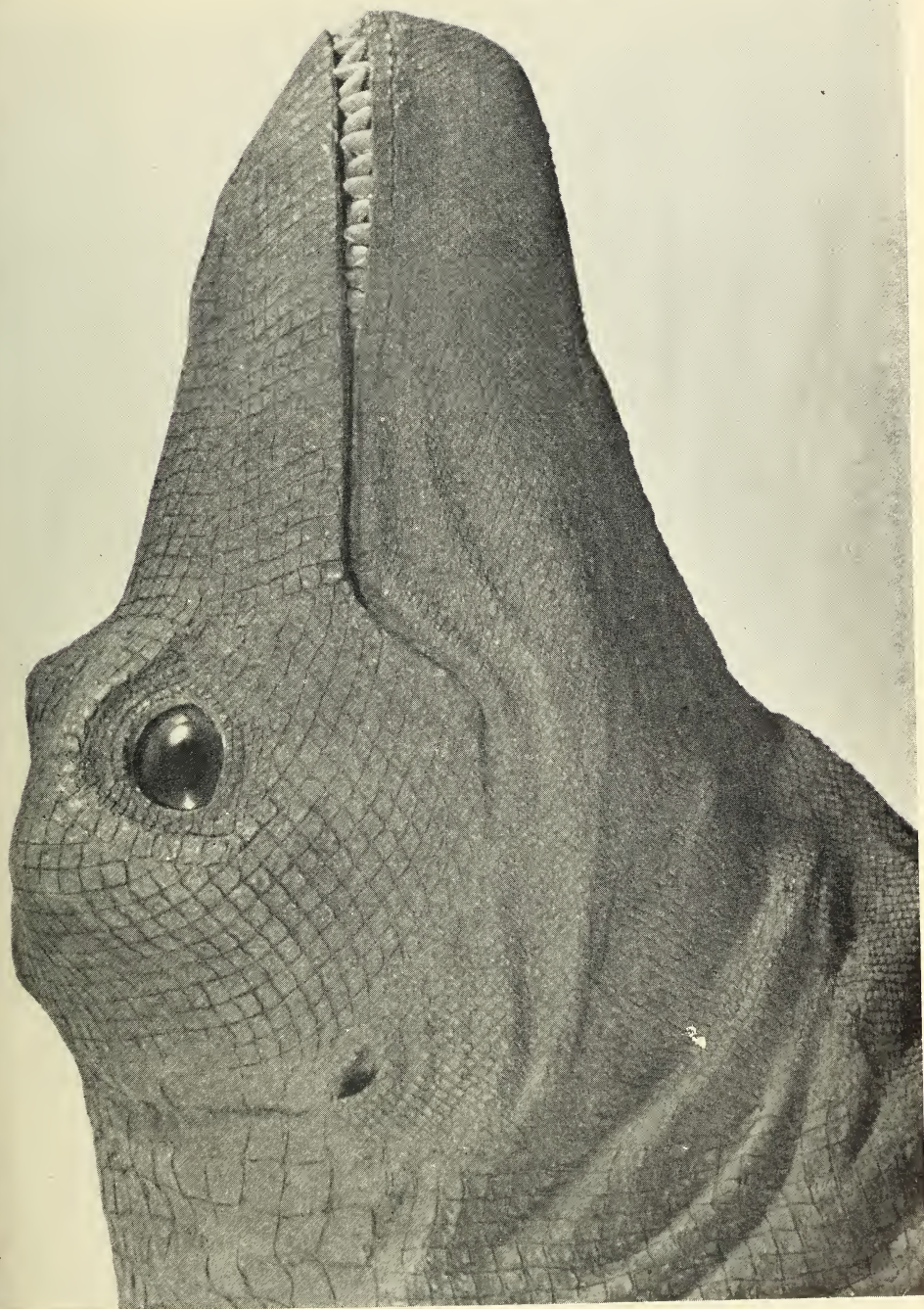
1. Snout of medium length, fairly high; facial surface not extending posterior to the anterior orbital border, transition on to cranial surface not abrupt but through a gentle curve.
2. Dorsal cranial surface fairly strongly pachyostosed, but centres of greatest thickening still distinct and the transition on to the face through a gentle curve and no transverse wall is thus formed.
3. Additional pachyostosis:
 - a. No distinct naso-frontal boss present, and from orbit to orbit the dorsal surface is evenly convex.
 - b. The parietal boss forms a rounded mound, highest round the pineal border but with its edges running into the general parietal surface.
 - c. Postorbital bar fairly wide and massive, though extending very far laterally it is dorsally not bulbous and flows evenly on to the generally thickened dorsal surface; the width over the postorbitals is very great and in dorsal view they form the lateral edge of the skull.
 - d. Posttemporal arch moderately thick and smooth.
 - e. Orbits just visible in dorsal view anterior to the postorbital bar which here forms the lateral border of the skull in dorsal view.
 - f. Antero-posterior diameter of the temporal fossa fairly great and thus broadly oval.
 - g. Dorsal parietal surface wide and laterally distinctly bayed.
4. Dentition well developed with 21 teeth of which 4 are in the premaxilla; there is an evenly graded decrease in size in posterior direction.
5. Quadrate not very far forward; the quadrate ramus of the pterygoid not extending posterior to the plane of the quadratic condyles, only underlying the anterior corner of the distal end of the stapes; quadrate with anterior process meeting the quadrate ramus of the pterygoid.
6. The lateral ramus of the pterygoid forms a strong and prominent bar and the width across the transverse rami is large.
7. The intersquamosal width is moderate, just more than the inter-postorbital width.
8. The basioccipital condyle is directed posteriorly.
9. The frontal is large and enters the orbital border, the supraoccipital is narrow and high, the tabular has a large occipital face and enters the posttemporal fossa, the lacrimal does not meet the nasal, the squamosal with a sharp anterior wedge into the jugal.

D. *Struthiocephaloides*⁹

1. Snout long, shallow, facial surface extending far back, posterior to the anterior orbital border, transition on to the cranial surface not abrupt.
2. Dorsal cranial surface strongly pachyostosed, but centres of greatest thickening still fairly distinct, but the transition on to the face not abrupt, with no indication of a transverse interorbital step.
3. Additional pachyostosis:
 - a. No naso-frontal boss (but with a swelling just anterior to the posterior end of the premaxilla in *cavifrons*).
 - b. Parietal boss distinct in *cavifrons* but in *duplessisi* undeveloped or indistinct due to confluence with the general pachyostosis of the parietal and frontal.
 - c. Postorbital bar very wide, massive, but without a bulbous boss in its dorsal part.
 - d. Posttemporal arch moderately to strongly thickened, fairly smooth.
 - e. Orbits just to plainly visible in dorsal view, and in dorsal view the post-orbitals do not form the lateral border of the skull.
 - f. Antero-posterior diameter of temporal fossa moderate to fairly large, fossa oval or narrow (in *cavifrons* the fossa lies obliquely in the skull).
 - g. Dorsal, parietal surface wide, laterally not pinched in.
4. Dentition well developed with 14 teeth of which 3 are in the premaxilla, and from the 5th the teeth gradually decrease in size.
5. Quadrate far forward, with the quadrate ramus of the pterygoid extending much posterior to the plane of the quadratic condyles.
6. The lateral ramus of the pterygoid forms a fairly strong and prominent bar but the width across the transverse rami is small.
7. The intersquamosal width is moderate to large.
8. The basioccipital condyle is directed much ventrally.
9. The frontal is fairly small, entering the orbital border in *duplessisi* but not in *cavifrons*, the tabular excluded from the temporal fossa, the lacrimal does not meet the nasal, the squamosal without anterior wedge in to the jugal.

E. *Struthionops*¹⁰

1. Snout fairly short and high, facial surface not extending posterior to anterior orbital border, transition to cranial surface not abrupt but through a gentle curve.
2. Dorsal cranial surface moderately pachyostosed, centres of greatest thickening distinct, no interorbital step.
3. Additional pachyostosis:
 - a. Naso-frontal boss very low and not confluent with the thickening on the prefrontals.
 - b. The parietal boss is a fairly prominent mound, highest round the pineal foramen and with its outer edges running into the general parietal surface.



RECONSTRUCTION OF STRUTHIOCEPHALUS
Photograph of the head of *Struthiocephalus* taken from the life-sized reconstruction in plaster of the whole animal as exhibited in the South African Museum. Modelled by the author.

- c. Postorbital bar fairly narrow and slender with dorsal swelling.
 - d. Posttemporal arch fairly weak and smooth.
 - e. Orbits large and well visible in dorsal view, postorbitals form the lateral border of the skull as seen in dorsal view.
 - f. Antero-posterior diameter of temporal fossa fairly large and broadly oval.
 - g. Dorsal parietal surface wide, but laterally slightly, pinched in.
4. Dentition with probably 14-15 teeth evenly decreasing in size in posterior direction.
 5. Quadrate not far forward.
 6. The lateral ramus of the pterygoid strong and prominent but transverse width across the rami moderate.
 7. The intersquamosal width is large, just more than the inter-postorbital width.
 8. The basioccipital condyle is not preserved.
 9. The frontal is large, but is just excluded from the orbital border, the lacrimal just meets the nasal, the squamosal without a wedge into the jugal.

DIAGNOSES FOR THE SPECIES OF STRUTHIOCEPHALUS

S. whaitsi

1. Naso-frontal, parietal and bulbous boss on postorbital prominent.
2. Snout moderately long, shallow and fairly weak.
3. Moderately broad over squamosals.
4. Pineal foramen moderately far from occipital border.
5. Postorbital bar wide.
6. Temporal fossa fairly rounded.
7. Median occipital ridge wedge-shaped with rounded edges.
8. Nares well back.
9. Quadrate well forward.
10. Interorbital width large.
11. Interparietal width small.
12. Posttemporal arch moderately strong.

S. rheederi

1. Naso-frontal, parietal and bulbous boss on postorbital prominent.
2. Snout fairly long, moderately shallow but broad.
3. Broad over squamosals.
4. Pineal foramen very near occipital border.
5. Postorbital bar probably wide (not evident from Broom's account).
6. Temporal fossa slit-like.
7. Median occipital ridge not figured or described by Broom.
8. Nares very far back.
9. Quadrate not figured or described by Broom.
10. Interorbital width very large.
11. Interparietal width large.
12. Posttemporal arch moderately strong.

S. milleri

1. Naso-frontal and parietal bosses very prominent and bulbous boss on postorbital bar moderately prominent.
2. Snout very long and very shallow.
3. Relatively narrow over squamosals.
4. Pineal foramen near occipital border.
5. Postorbital bar narrow.
6. Temporal fossa fairly rounded.
7. Median occipital ridge not figured or described by Olson and Broom.
8. Nares fairly near premaxillary edge.
9. Quadrate not figured or described by Olson and Broom.

10. Interorbital width small.
11. Interparietal width fairly small.
12. Posttemporal arch robust.

S. akraalensis

1. Naso-frontal boss large but low, parietal boss prominent, postorbital bar dorsally greatly thickened with the development of a longitudinal ridge raised above the surface of the frontal which thus appears excavated.
2. Snout very long and shallow.
3. Broad over the squamosals.
4. Pineal foramen far from occipital border.
5. Postorbital bar very wide and strongly rugose.
6. Temporal fossa slit-like.
7. Median occipital ridge straight with sharp median edge.
8. Nares far back.
9. Quadrates very far forward.
10. Interorbital width very large.
11. Interparietal width very large.
12. Posttemporal arch very robust.

THE CHIEF MEASUREMENTS COMPARED

	<i>whaitsi</i>	<i>rheederi</i>	<i>milleri</i>	<i>akraalensis</i>
Length	558	624	480	655
Width	345	432	300	390
Interorbital width	170	180	130	175
Interparietal width	100	140	115	167
Pineal foramen to occipital edge	65	48	44	90
Naris to Pr. Mx. edge	85	114	52	95

KEYS TO FACILITATE RAPID TAXONOMIC IDENTIFICATION

- Deinocephalia.** Large therapsids, with pachyostosed skulls, with large quadrates, quadratojugals forming the corner of the 'cheek', premaxillaries with long facial exposure.
- Titanosuchia.** Deinocephalians with differentiated carnivorous dentition, cranial bones not greatly pachyostosed, snout long, low parietal crest, quadrates not situated far anteriorly.
- Tapinocephalia.** Medium-sized to large Deinocephalians with undifferentiated herbivorous dentition, cranial bones slightly to very greatly pachyostosed, in all but the Moschosaurids the snout is weakened, there is no parietal crest (except in *Riebeeckosaurus* and *Auenantia*); the quadrates are situated moderately to very far anteriorly.

GROUPS IN THE TAPINOCEPHALIA

1. Little pachyostosis *Moschosaurus*-group
2. Great pachyostosis 3
3. Facial bones thickened to run evenly on to the cranial surface *Moschops*-group
4. Facial bones not so thickened as to run evenly on to the cranial surface 5
5. Snout very much shortened and weakened *Tapinocephalus*-group
6. Snout not very much shortened and weakened *Mormosaurus*-group

GENERA OF THE MORMOSAURUS-GROUP

1. Skull with abrupt step from face to cranial surface *Mormosaurus*
2. Skull without abrupt step 3
3. Distinct naso-frontal boss present *Struthiocephalus*
4. Distinct naso-frontal boss absent 5
5. Width over postorbitals not very great and postorbitals not forming lateral edge of skull in dorsal view *Struthiocephaloides*
6. Width over parietals great and postorbitals forming lateral edge of skull in dorsal view 7
7. Width across jugals much less than across postorbitals *Tawocephalus*
8. Width across jugals not much less than across postorbitals *Struthionops*

THE SPECIES OF STRUTHIOCEPHALUS

- | | |
|--|--------------------|
| 1. Snout very long and very shallow | <i>milleri</i> |
| 2. Snout not very long and very shallow | 3 |
| 3. With prominent ridge median to postorbital boss | <i>akraalensis</i> |
| 4. Without this ridge | 5 |
| 5. Pineal foramen very near occipital border | <i>rheederi</i> |
| 6. Pineal foramen not near occipital border | <i>whaitsi</i> |

DISCUSSION

It would be unwise to attempt a discussion of the relationships of the Deinocephalians with other orders and *inter se* until all the material in the South African Museum has been studied. At this stage I am confining my remarks to some points which the study of *Struthiocephalus* has brought to the fore.

Age in the Struthiocephalus skull

A specimen of *whaitsi* (S.A.M. 11493) has a skull just as long as that of the type (S.A.M. 2678) and another specimen referred to this species (S.A.M. 11591), but in it the upper teeth are just commencing to erupt and the outer edge of both premaxillaries and maxillaries is sharp and appears to form a functioning cutting edge until the teeth are fully erupted. All the cranial bones are still little affected by any pachyostosis. The postorbital bar is narrow and lightly built with only its dorsal part slightly expanded and here the postfrontal is large and has not yet overgrown the postorbital. The posterior flange of the postorbital forming the dorsal border of the temporal fossa is little reduced and though not meeting the squamosal extends far posteriorly and is not encroached on or overhung by the parietal. The antero-posterior diameter of the temporal fossa is nearly equal to the dorso-ventral diameter. The posttemporal arch is not thickened and does not encroach into the fossa. The quadrates still lie in a plane posterior to the anterior orbital border. The whole outer surface is still smooth and free from rugosities. Unfortunately the state of preservation does not reveal the structure of the occiput and the ventral aspect of the skull. What could be determined in this juvenile skull is however sufficient to show that many of the characters peculiar to the adult Tapinocephalian skull are mainly due to the pachyostosis which increasing age brings about and which obscures its essential therapsid nature.

The Cranial Pachyostosis

Apart from the fact that in both *Moschops* and *Struthiocephalus* an intensification of the thickening of the cranial bones takes place during the life of the individual, it also appears to be a process that can be traced phyletically.

In *Moschosaurus*, which is undoubtedly the most primitive of the South African Tapinocephalians, there is very little pachyostosis and in *Agnosaurus* it is also slight, whereas in all the other known forms a lesser or greater degree of bone-thickening is apparent. Less of the skull is affected in the *Mormosaurus*-group than in the *Moschops*- and *Tapinocephalus*-groups. The thickening chiefly affects the supra- and interorbital region, the intertemporal skull roof, the post-orbital bar; the posttemporal arch and the face and 'cheek' are relatively little